

GROWTH STRATEGIES OF FISH LARVAE

by

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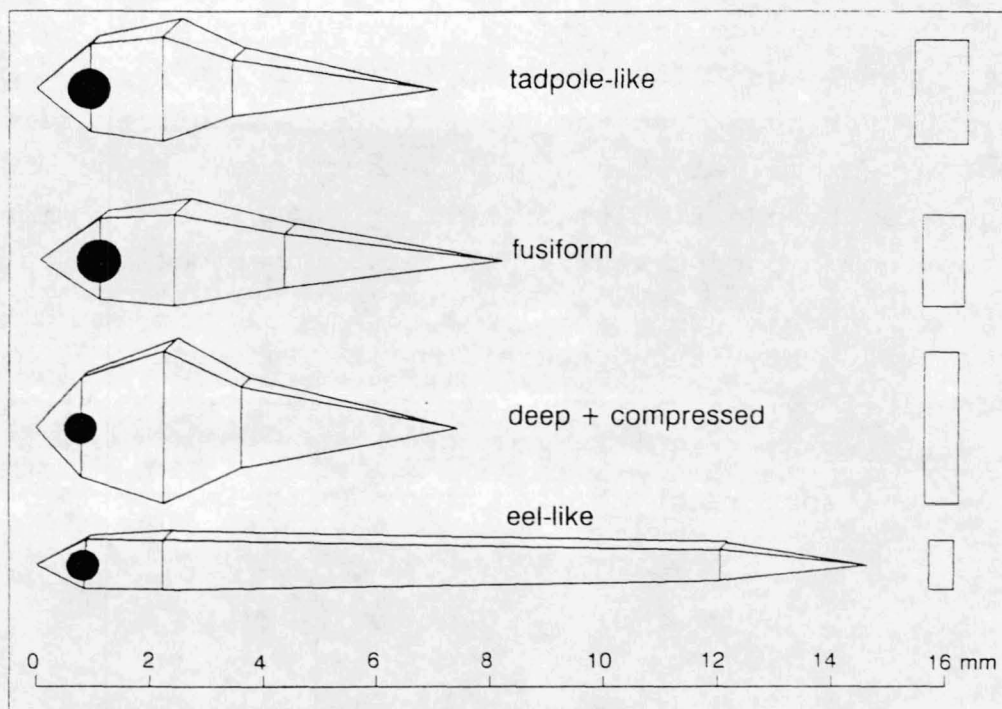
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ABSTRACT

Ten morphometric distances were measured on 831 fish larvae from 33 species and 18 families. Volume was calculated from these measurements and the shape of all larvae with a volume between 3 and 5 μl was compared. It became possible then to group the larvae around four characteristic shapes: eel-like larvae, deep + compressed larvae, fusiform larvae, and tadpole-like larvae. Net drawings were constructed from the average morphometric distances of each group. At a given volume, eel-like larvae are about twice as long as larvae from other groups, which are of about the same length. Tadpole-like larvae are wider, and deep + compressed larvae are deeper than the others. The diameter of the eye is larger and the lateral surface area is smaller in tadpole-like and in fusiform larvae than in deep + compressed and eel-like larvae. The total surface area decreases for larvae of the same volume in the following sequence: eel-like > deep + compressed > fusiform > tadpole-like. Volume is a better indicator for comparable stages of postlarval development than length, especially when eel-like larvae like anchovy or herring are compared with other larvae. As a hypothesis, two different growth strategies are suggested: A) Eel-like larvae and deep + compressed larvae grow slowly while feeding on abundant small prey items. Mortality caused by predation is reduced by their ability for burst escapes, as well as by their extreme length and depth, respectively, which makes them appear bigger than suggested by their volume. Their energy saving swimming style gives them a good potential to survive periods of starvation. B) Fusiform and tadpole-like larvae represent fast-growing predators. They invest energy to speed through the phase of high vulnerability. If, however, appropriate prey items are scarce, this strategy fails, and because of their high energy consumption they will soon reach the "point of no return".

1 Introduction

MOSER (1981) demonstrated for several fish species the striking difference in body shape between larvae and adults. Fish larvae change their morphometric proportions during development and in metamorphosis to obtain the shape of the adults (FUIMAN 1983). The aim of this study is to examine different growth strategies of fish larvae: Do they grow isometrically or do they invest tissue buildup preferably into growth in length, width, or depth? Thus, it would be desirable to compare fish larvae with equal cell numbers, as is done in the early stages of ontogeny. Cell counts are not available, but dry weight of fish larvae is highly correlated with DNA content (CLEMMESSEN 1985). Dry weight itself is highly correlated with wet weight, which can be replaced by volume. Volume can be estimated from morphometrical measurements (WINBERG 1971). In this study, volume will be used to compare morphometric proportions of various species of fish larvae.

Various authors have used descriptions such as eel-like, fusiform, tadpole-like, or deep + compressed to describe groups of fish larvae with similar shapes (RUSSELL 1976; HALBEISEN 1988; HUNTER 1981). This study attempts to reproduce such a classification on the basis of morphometric measurements. The ecological importance of shape in fish larvae is discussed.

Throughout this paper, the postlarval phase is defined as the phase from first feeding to metamorphosis.

2 Materials and Methods

Most of the fish larvae used in this study were collected in the Celtic Sea in April 1986 during a cruise of R/V "Poseidon" (RÖPKE 1989). A smaller part of the material was obtained from collections of fish larvae at the Institut für Meereskunde, Kiel. All larvae were stored in a buffered solution of 4 % formaldehyde in freshwater for at least two years prior to measurement. Taxa, sample size, and length range are summarized in Table 1. Ten

variables were measured for each larva using a video system (FROESE 1988, 1989, 1990): standard length, prepectoral length, body width at pectorals, body width at anus, preorbital length, vertical diameter of eye, vertical body depth through center of eye, vertical body depth at pectorals origin, vertical body depth at anus.

Table 1: Species considered in this study, with acronyms, sample size and range of standard length

Species	Acronym	N	Standard length (in mm)
1. <i>Clupea harengus</i>	cluphare	50	6.8 - 19.4
2. <i>Argentina sphyrena</i>	argesphy	48	4.9 - 18.5
3. <i>Benthoosema glaciale</i>	bentglac	52	4.0 - 8.1
4. <i>Merluccius merluccius</i>	merlucci	45	3.1 - 7.2
5. <i>Gadiculus argenteus</i>	gadiarge	52	2.5 - 7.3
6. <i>Merlangius merlangus</i>	merlangi	52	2.3 - 8.0
7. <i>Micromesistius poutassou</i>	micrpout	30	3.5 - 9.6
8. <i>Pollachius pollachius</i>	pollpoll	51	3.1 - 11.7
9. <i>Trisopterus spec.</i>	trisspec	51	4.5 - 11.9
10. <i>Molva molva</i>	molvmolv	38	3.2 - 6.7
11. <i>Scomber scombrus</i>	scomscom	45	2.9 - 9.2
12. <i>Callionymus spec.</i>	callspec	69	1.9 - 4.2
13. <i>Triglidae</i>	triglida	37	4.2 - 15.2
14. <i>Lepidorhombus boscii</i>	lepibosc	41	3.5 - 8.0
15. <i>Lepidorhombus whiffiagonis</i>	lepiwhif	43	3.5 - 12.7
16. <i>Microchirus variegatus</i>	micrvvari	31	2.3 - 7.0

Net drawings of each larva were created, and the volumes were calculated (Fig. 3) (FROESE 1990). Under the assumption that volume can be replaced by weight, a theoretical length was derived from the calculated volume: The relationship between weight and length in fish is described as:

$$W = a * L^b$$

where W = weight, a = specific form factor, L = length, and b = allometric coefficient. Isometric growth of length with weight occurs if b = 3. Setting the value a = 1 and b = 3 and solving the equation for L leads to:

$$L_{Vol} = W^{1/3}$$

where L_{Vol} = an artificial length which grows isometrically with weight and volume. This length can be used as reference parameter to check for allometric growth of the other morphological distances including standard length.

3 Results

To compare the body proportions of different species of fish larvae, all individuals with a calculated volume of 3 to 5 μ l were selected from the data; for every species the average depth and width at pectorals were plotted against standard length (Fig. 1 + 2). The plots reveal four clearly separated form groups of larvae: eel-like larvae, deep + compressed larvae, tadpole-like larvae, and fusiform larvae.

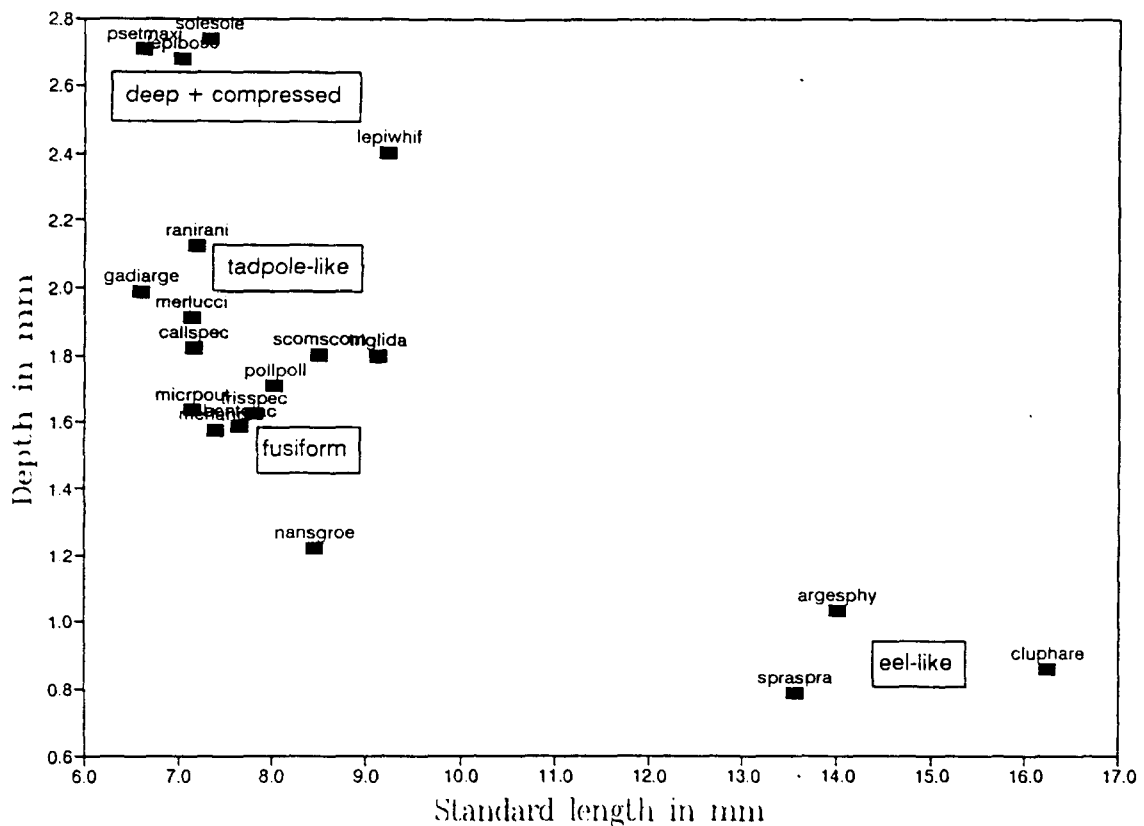


Figure 1: Relationship between depth and standard length for fish larvae with a volume of 3 - 5 μ l.

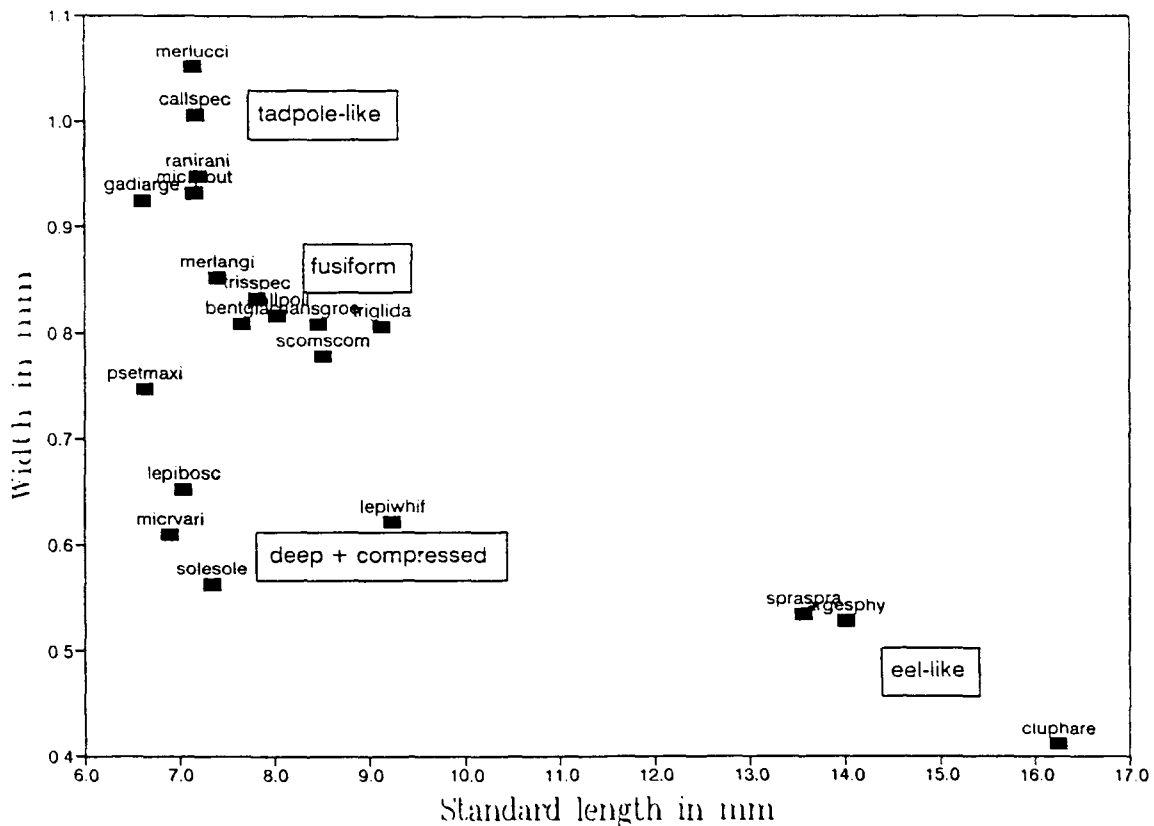


Figure 2: Relationship between width and standard length for fish larvae with a volume of 3 - 5 μ l.

To obtain a visual impression of the form types, net drawings were constructed from the average morphometric distances for each group (Tab. 2 and Fig. 3). From these data the following generalizations were derived: eel-like larvae are about twice as long as the others, which are of about the same length. Tadpole-like larvae are significantly wider and deep + compressed larvae are significantly deeper than the others. The diameter of the eye is significantly larger and the lateral surface area is significantly smaller in tadpole-like and fusiform larvae than in deep + compressed and eel-like larvae (median test, 95% confidence limit). The total surface area decreases in the following sequence: eel-like > deep + compressed > fusiform > tadpole-like.

Table 2: Means of distances for all fish larvae with a volume of 3 - 5 μ l.

Species	Standard length mm	Prepec. length mm	Width at pec. mm	Width at anus mm	Preal length mm	Preorb. length mm	Diameter of eye mm	Depth at eye mm	Depth at pec. mm	Depth at anus mm	Volume μ l	Lateral area mm ²	Total area mm ²
<i>Argentina sphyrena</i>	14.00	2.57	0.53	0.36	10.94	0.62	0.67	1.09	1.03	0.49	3.75	9.38	28.72
<i>Clupea harengus</i>	16.24	2.18	0.41	0.32	13.67	0.57	0.57	0.77	0.86	0.61	3.59	10.67	31.49
<i>Sprattus sprattus</i>	13.56	1.85	0.53	0.30	11.53	0.52	0.49	0.70	0.79	0.52	3.14	7.89	25.49
eel-like	14.60	2.20	0.49	0.33	12.05	0.57	0.57	0.85	0.89	0.54	3.49	9.31	28.56
<i>Lepidorhombus boscii</i>	7.04	2.24	0.65	0.45	3.38	0.65	0.52	1.83	2.68	1.37	3.57	8.69	21.75
<i>Lepidorhombus whiff.</i>	9.23	2.69	0.62	0.45	4.41	0.78	0.56	1.90	2.40	1.15	4.16	10.38	26.43
<i>Microchirus variegatus</i>	6.90	2.00	0.61	0.33	3.41	0.35	0.42	1.59	3.06	1.14	3.28	8.76	21.23
<i>Psetta maxima</i>	6.64	2.36	0.75	0.42	3.66	0.52	0.69	1.80	2.71	2.14	4.63	10.46	25.44
<i>Solea solea</i>	7.33	2.24	0.56	0.38	3.29	0.45	0.44	1.70	2.74	1.33	3.13	8.95	21.67
deep + compressed	7.43	2.31	0.64	0.40	3.63	0.55	0.53	1.76	2.72	1.43	3.75	9.45	23.30
<i>Benthosema glaciale</i>	7.65	2.01	0.81	0.61	4.10	0.55	0.65	1.26	1.59	1.15	4.02	7.10	20.98
<i>Merlangius merlangus</i>	7.40	2.41	0.85	0.66	3.76	0.67	0.72	1.58	1.58	0.98	3.58	6.53	19.57
<i>Nansenia groenlandica</i>	8.46	2.27	0.81	0.35	6.43	0.56	0.68	0.93	1.22	0.54	3.28	6.09	19.57
<i>Pollachius pollachius</i>	8.03	2.51	0.82	0.73	4.06	0.59	0.76	1.62	1.71	1.11	4.36	7.76	22.87
<i>Scomber scombrus</i>	8.50	2.24	0.78	0.49	3.77	0.57	0.84	1.61	1.80	1.09	3.61	7.70	21.38
<i>Triglidae</i>	9.13	2.66	0.81	0.53	4.14	1.05	0.77	1.70	1.80	0.86	3.78	7.50	21.74
<i>Trisopterus spec.</i>	7.80	2.33	0.83	0.64	3.71	0.61	0.80	1.43	1.63	1.07	3.70	6.79	20.20
fusiform	8.14	2.35	0.81	0.57	4.28	0.66	0.74	1.45	1.62	0.97	3.76	7.07	20.90
<i>Callionymus spec.</i>	7.17	2.45	1.01	0.66	3.83	0.59	0.73	1.41	1.82	0.80	4.01	6.24	19.45
<i>Gadiculus argenteus</i>	6.60	2.12	0.93	0.66	3.32	0.61	0.74	1.66	1.99	1.07	3.89	6.48	18.99
<i>Merluccius merluccius</i>	7.14	1.95	1.05	0.77	3.15	0.65	0.70	1.67	1.91	1.10	4.45	6.53	20.36
<i>Micromesistius poutassou</i>	7.16	2.29	0.93	0.82	3.53	0.62	0.73	1.48	1.64	0.99	3.93	6.18	19.63
<i>Raniceps raninus</i>	7.19	2.12	0.95	0.47	3.31	0.35	0.67	1.64	2.13	1.13	3.91	7.38	20.30
tadpole-like	7.053	2.185	0.972	0.675	3.427	0.565	0.716	1.572	1.897	1.016	4.039	6.564	19.745

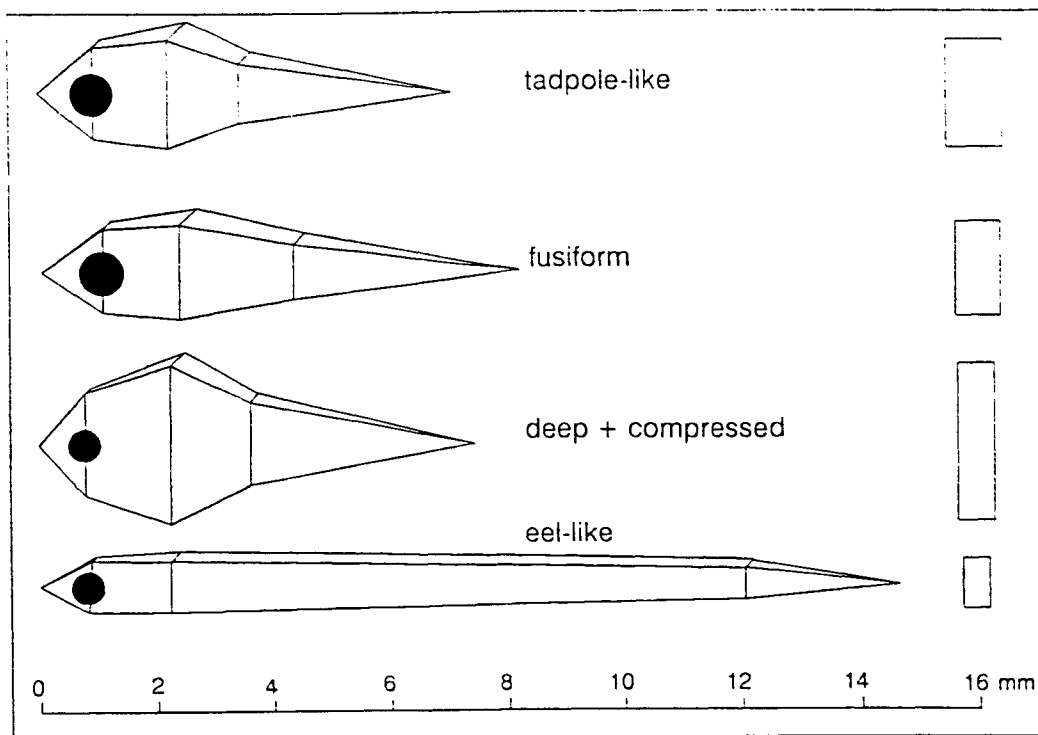


Figure 3: Shapes of fish larvae with a volume of 3 - 5 μ l. The rectangles represent the cross-section at the pectorals.

To obtain an impression of the variance within the form groups, standard length and depth and width at pectorals were plotted against L_{Vol} (Fig. 4 - 7).

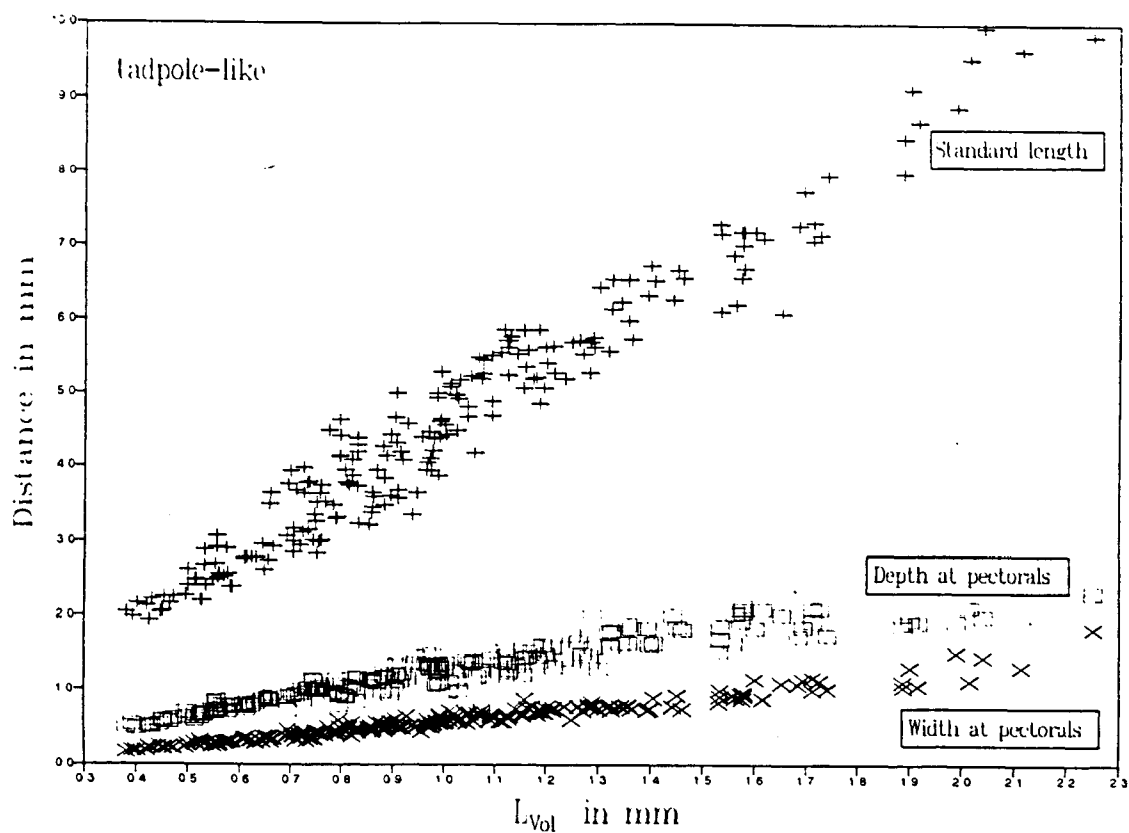


Figure 4: Growth of standard length and depth and width at pectorals for tadpole-like fish larvae.

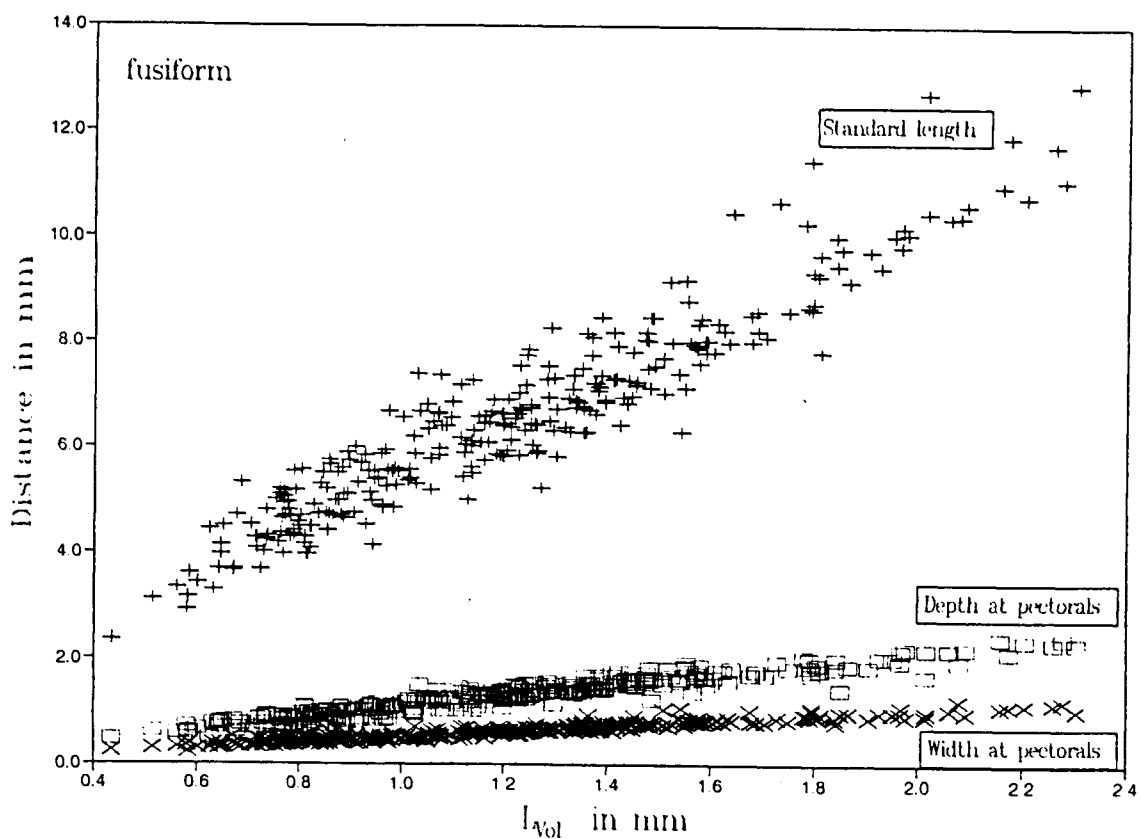


Figure 5: Growth of standard length and depth and width at pectorals for fusiform fish larvae.

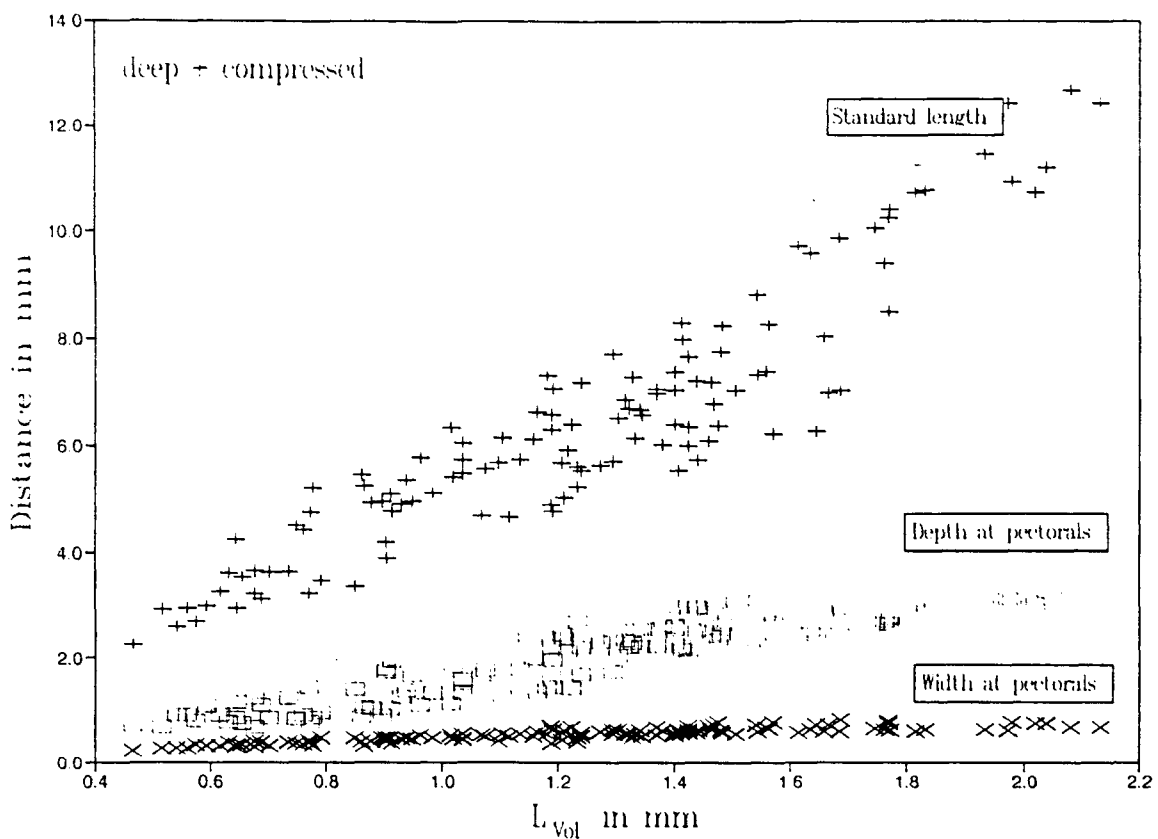


Figure 6: Growth of standard length and depth and width at pectorals for deep + compressed fish larvae.

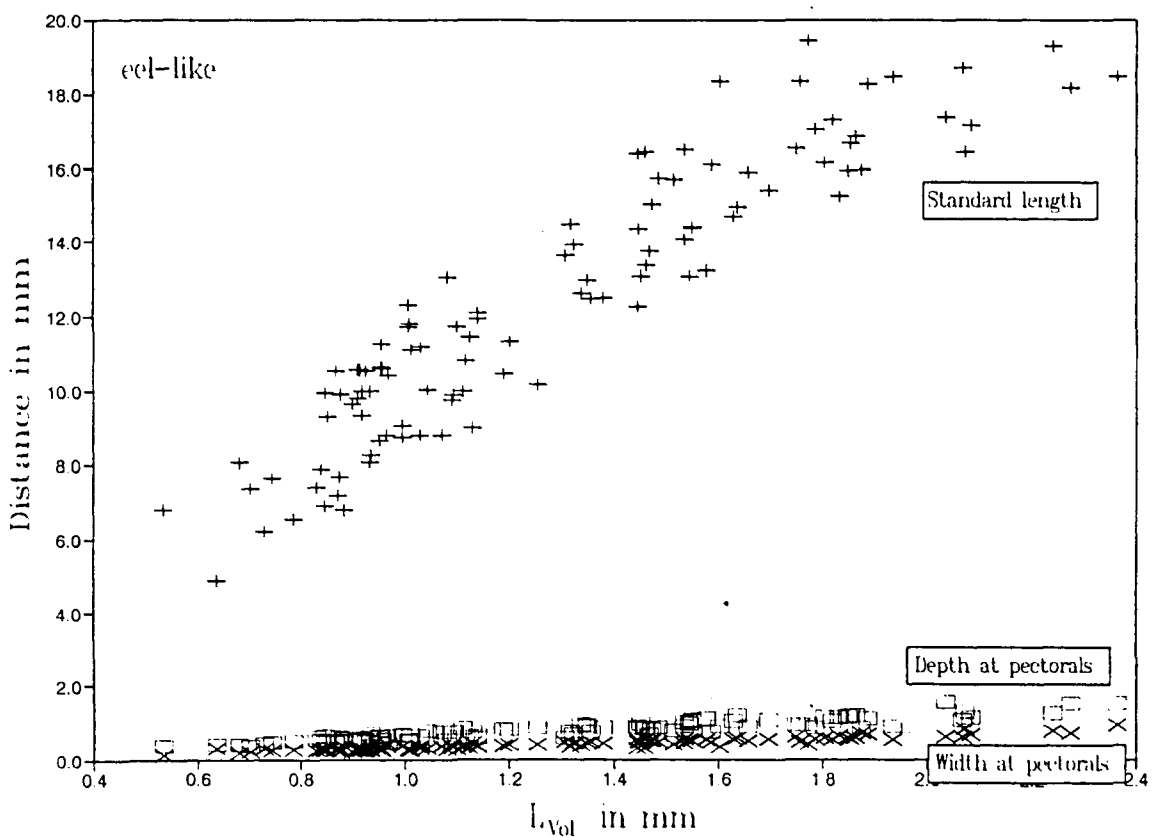


Figure 7: Growth of standard length and depth and width at pectorals for eel-like fish larvae.

4 Discussion

4.1 Length or volume as indicator for stage of development?

Morphological, physiological and ethological characters of fish larvae change considerably in the course of larval development (BLAXTER 1986). It is very important to base a comparison of these characters between different species on larvae of the same stage of development. Traditionally, standard length or total length have been used to compare fish larvae, but fish larvae of the same length may be in completely different stages of development: While in *Clupea harengus* first dorsal fin rays only begin to develop at a length of 14 mm, *Scomber scombrus* enters metamorphosis at that length with all fins well developed (RUSSELL 1976). Comparing a 20 mm herring with a 20 mm mackerel would mean to compare a postlarva with a juvenile.

Table 3: Length and calculated volume at first feeding of selected fish larvae after RUSSELL (1976) and FROESE (1990).

Species	Length mm	Volume μl
<i>Clupea harengus</i>	8 - 10	0.70
<i>Argentina sphyrena</i>	8 - 8.5	0.82
<i>Scomber scombrus</i>	4.5	0.65
<i>Merluccius merluccius</i>	4.0	0.68
<i>Microchirus variegatus</i>	4.0	0.74
<i>Callionymus lyra</i>	2.3	0.22

As deducted above, volume is proposed as a better estimator for similar stages of development of postlarvae. Table 3 shows that at first feeding, *Clupea harengus* and *Argentina sphyrena*, the two members of the eel-like group, are about twice as long as *Scomber scombrus*, *Merluccius merluccius*, and *Microchirus variegatus*, whereas the calculated volume of these five species is similar. While these results suggest that fish larvae of the North Sea and adjacent waters have different lengths, but similar volumes at the time of first feeding, there is an obvious exception to the rule: *Callionymus lyra* is characterized by a very small length at

the time of yolk absorbtion (RUSSELL 1976), and also has a very small volume.

The unsuitability of length as an indicator of developmental stage is also demonstrated by the following facts:

- At hatching, the first marked stage of larval development, length for the eel-like Clupeidae listed in FAHAY (1983) ranges from 2.4 to 10 mm, compared to 1.4 to 5.7 mm for the fusiform Gadidae. The fusiform *Scomber japonicus* measures about 3.5 mm at hatching, whereas the eel-like *Engraulis mordax* measure about 5 to 5.5 mm (SCHUMANN 1965).
- At the time of first feeding, the second marked stage of development, the eel-like Clupeidae listed in FAHAY (1983) range from 5.8 to 8 mm compared to the fusiform or tadpole-like Gadidae, which range from 3.6 to 5 mm.
- At metamorphosis, the last marked stage of larval development, the fusiform *Scomber japonicus* measures 14.5 mm whereas the eel-like *Engraulis mordax* measures 32 mm (HUNTER 1980).
- HEWITT (1981) shows that anchovy are about twice as long as mackerel throughout the postlarval phase (Fig. 8).

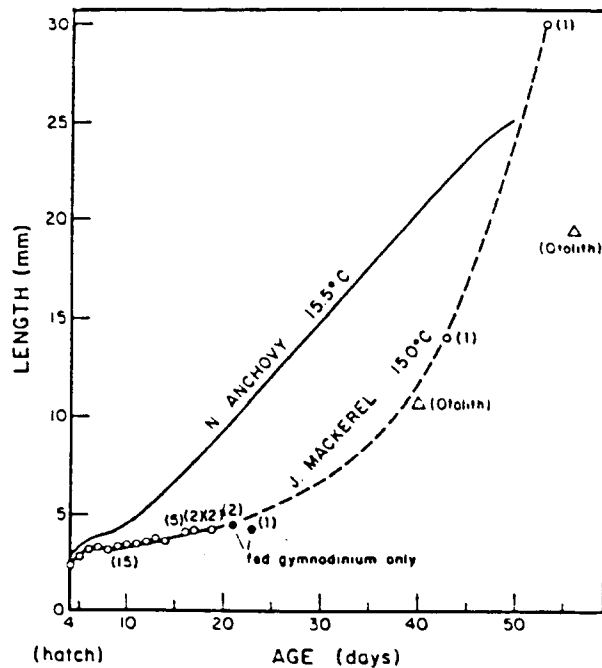


Figure 8: Growth in length over time for *Engraulis mordax* and *Scomber japonicus* (after HEWITT 1981).

If volume is a better indicator for comparable stages of larval development, then some results from the literature will have to be revised. For example, BLAXTER (1986, page 104) compares cruising speeds of 8 species of fish larvae over length (Fig. 9, A), showing that larvae of the eel-like group (*Clupea harengus harengus*, *Clupea harengus pallasii*, *Coregonus clupeaformis*, *Engraulis mordax*) swim more slowly than larvae of the other groups (*Micropterus salmoides*, *Perca flavescens*, *Pleuronectes platessa*, *Scomber japonicus*, *Stizostedion vitreum vitreum*) at all stages of development (see also HUNTER, 1981). However, when anchovy and herring are plotted over a second X-axis that has been corrected by a factor of 0.5, thus comparing, e.g., an 8 mm fusiform larvae with a 16 mm eel-like larvae (Fig. 9, B), it turns out that there is no remarkable difference in cruising speed in the first half of the postlarval phase. It is only in the second half of the postlarval phase that cruising speed of anchovy and herring is slower. This result is in good accordance with WEBB and WEIHS (1986), who expect an advantage in cruising speed for thunniform larvae only after differentiation of the

caudal fin. BALON (1975) explicitly divides the postlarval phase into a period before and a period after the development of fin rays.

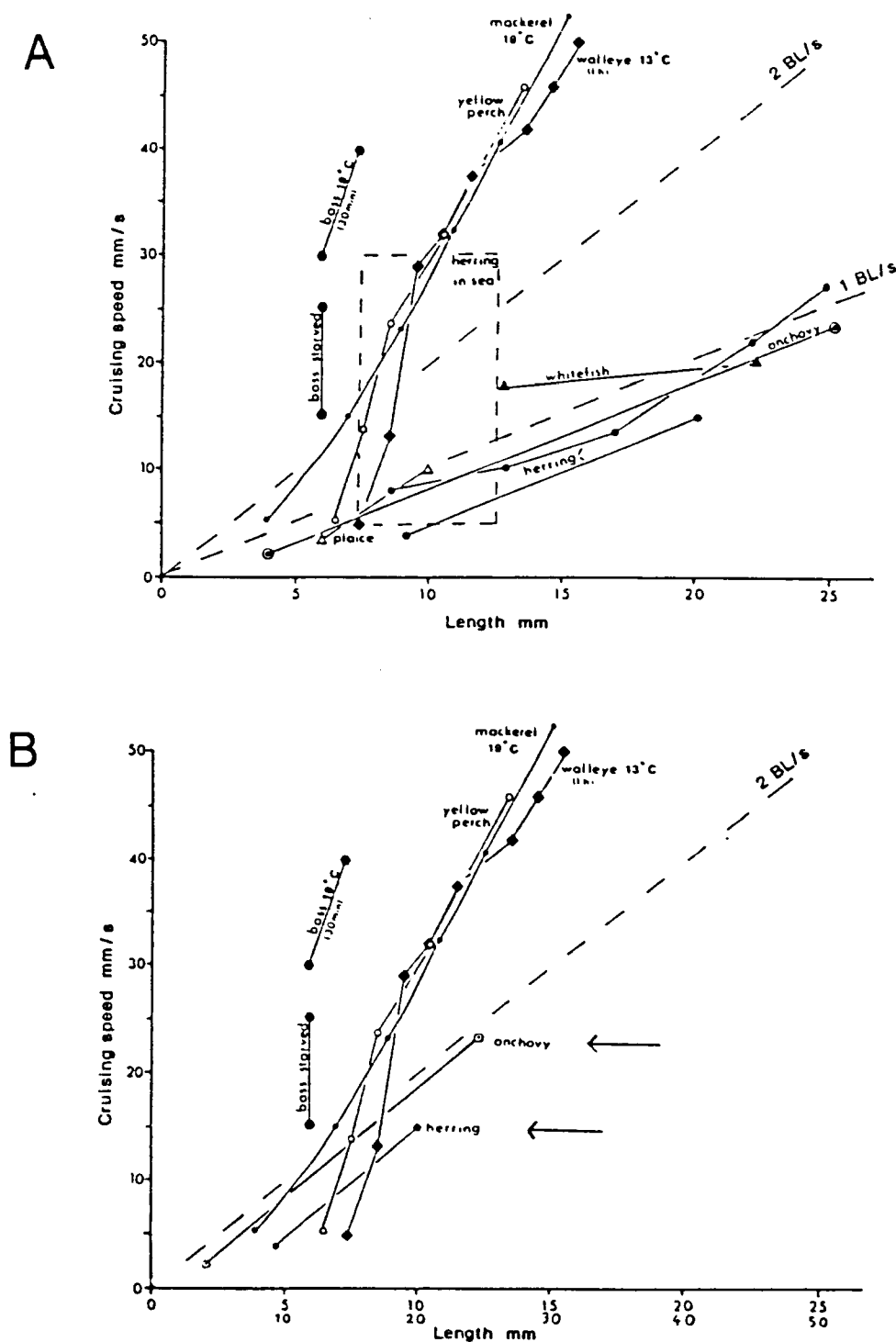


Figure 9: Relation between cruising speed and length for several species of fish larvae. A = unchanged after BLAXTER (1986), B = with second X-axis for anchovy and herring.

Another example is shown in figure 10 A, in which mouth width is plotted over length for six species of fish larvae (HUNTER 1981). The figure suggests that the eel-like anchovys have a smaller mouth width than the other species, but a correction of the X-axis for anchovys by the factor 0.5 leaves no significant difference in mouth width between the eel-like larvae and the others.

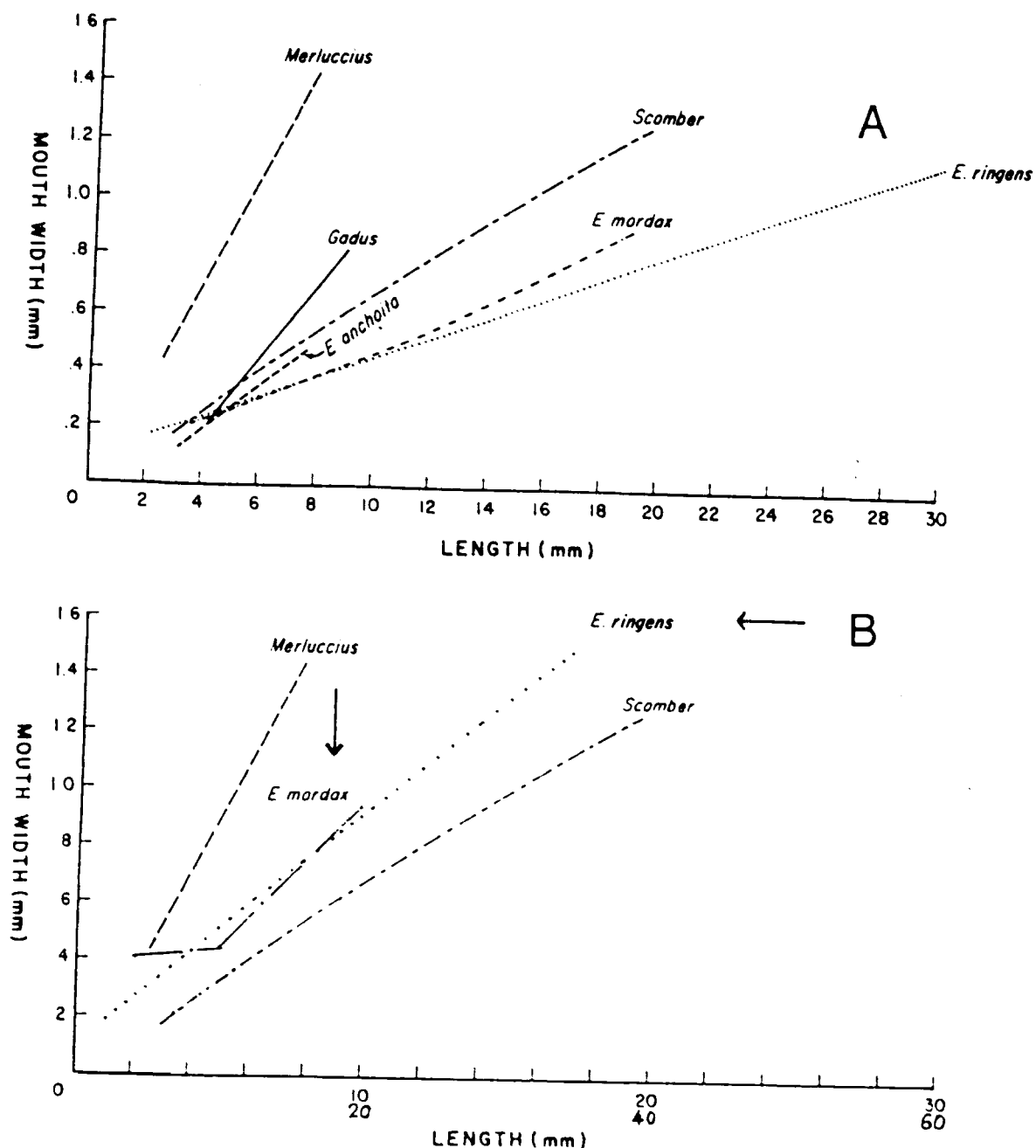


Figure 10: Relation between mouth width and length for several species of fish larvae. A = unchanged after HUNTER (1981), B = with second X-axis for anchovys.

In summary it appears that volume rather than length should be used as indicator of postlarval development. This holds especially true when eel-like larvae like anchovy or herring are compared with other larvae.

4.2 Growth strategies of fish larvae: The ecological importance of shape

In the context of this study, growth strategy is defined as the specific pattern of allometric or isometric growth of the morphometric distances measured, resulting in a specific shape of the body.

The results of this study suggest that there is no random assortment of body shapes in different species. Instead, fish larvae can be grouped into a few characteristic shapes: eel-like larvae (e.g. clupeids and anchovys), deep + compressed larvae (e.g. flatfish), tadpole-like larvae (e.g. Callionymidae, Merlucciidae, and some Gadidae), and fusiform larvae (e.g. Scombridae and most Gadidae). Figures 4 - 7 show little variance for the 3 to 7 species included in each of these groups.

Important characteristics related to body form, such as swimming and feeding behaviour should be similar within a group. If this assumption is generalized, then characteristics identified in some members of the group may be regarded as a common feature of all. An analysis of the literature leads to the conclusion that fish larvae may be grouped into two categories with similar features: A) eel-like larvae and deep + compressed larvae, and B) tadpole-like larvae and fusiform larvae:

A) Eel-like and deep + compressed larvae

Eel-like and deep + compressed larvae have large surface areas and small eyes. Most of them look very different from the adults. They swim more slowly in the second half of the postlarval phase than other larvae (Fig. 9), but they are capable of explosive swimming bursts (BLAXTER 1986, WEBB and WEIHS 1986, ROSENTHAL and HEMPEL 1970) which are advantageous for attack and escape (WEBB

and COROLLA 1981; BLAXTER and BATTY 1985). Eel-like larvae have maneuvering problems and do not attack the same prey twice (BLAXTER and STAINES 1971), which could explain why they prefer small prey organisms (HUNTER 1981) despite having a mouth width similar to that of the other larvae (Fig. 10). In spite of two reports from the laboratory (BROWNELL 1984, OIESTAD 1985), there is no indication of in situ cannibalism or piscivory for the postlarvae of these groups. HUNTER (1981, page 41) gives the following description of their feeding behaviour: "Upon sighting a prey, a clupeoid larva forms a sinuous posture and advances towards the prey by sculling the pectoral fins and undulating the finfold while maintaining the body in the S-posture. When the prey is a short distance from the snout, the larva opens its mouth, straightens its body to drive forward, and engulfs the prey." A similar feeding behaviour is reported for deep + compressed larvae (RILEY 1966, HOUDE 1972). The larvae of this group do not swim continuously, but perform a constant change between active swimming and feeding and passive gliding (ROSENTHAL and HEMPEL 1970, RYLAND 1963, SCHUMANN 1965, HUNTER 1972). This is regarded as energetically advantageous (VLYMEN 1974). Stomach analyses (ARTHUR 1976) suggest that the small eyes limit their ability to hunt during dusk and dawn. The larvae of this group grow more slowly than fusiform larvae (THEILACKER and DORSEY 1980).

B) Tadpole-like and fusiform larvae

Tadpole-like larvae concentrate their body mass in a big head whereas fusiform larvae already have the typical shape of the adults. Both have large eyes. Because of their small surface area they consume little energy when swimming slowly (WEBB and WEIHS 1986). On the other hand, the small surface area limits their oxygen uptake, which in turn limits their growth (PAULY 1981); they must swim to improve the efficiency of the respiratory surface. Tadpole-like and fusiform larvae feed in a manner typical of many adult fishes (HUNTER 1981, page 41): "Upon sighting a prey, the larva advances towards the prey, stops,

draws back the tail, and holds it in a slightly recurved high amplitude position. The rest of the body is straight; feeding is accomplished by opening the mouth and driving the tail posteriorly." These larvae possess a good manouvering capability and will attack the same prey several times (BLAXTER and STAINES 1971). They are well prepared to successfully exploit short-time aggregations of prey (HOUDE and SCHEKTER 1978) or attack large prey organisms (ARTHUR 1976). Fish larvae, including their own species, are part of the normal diet (GRAVE 1981; HUNTER and KIMBRELL 1979; LAURENCE et al. 1981; LIPSKAYA 1982; NELLEN 1986; OIESTAD 1985). Their large eyes should be advantageous for hunting and escaping during dusk and dawn. Altogether, tadpole-like and fusiform larvae seem to represent a more modern type of fish larva.

4.3 Two strategies for survival

The two groups seem to represent two different strategies for survival: Group A) accepts the disadvantages of slow growth for the advantage of feeding on abundant small prey items. Mortality caused by predation should be reduced by their ability for burst swimming as well as by their extreme length and depth, respectively, which makes them appear bigger than corresponds to their volume. Their energy-saving swimming style should enable them better to survive periods of starvation.

The strategy of group B) is described by HUNTER (1981) as "large prey - fast growth". These larvae represent fast-growing predators. They invest energy to speed through the phase of high vulnerability. If, however, appropriate prey items are scarce, this strategy fails, and because of their high energy consumption they could soon reach the "point of no return".

4.4 Conclusions

The ideas presented here are based on analysis of a limited number of species, and on limited knowledge on behaviour of fish larvae. There might well be more categories of fish larvae, for

example, elongated larvae such as *Glyptocephalus cynoglossus* or for box-like larvae such as *Zeus faber*. There might also well be differences between eel-like larvae and deep + compressed larvae that preclude their pooling into one group. The ideas presented in this paper therefore remain hypothetical, pending verification.

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